

Chromosome numbers in eight species of Palaearctic Psocoptera (Insecta)

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Abstract. Karyotypes of eight Psocoptera species are reported for the first time. In *Valenzuela oyamai* (Enderlein, 1906) (Caeciliusidae), *Peripsocus golubae* Lienhard, 2006 (Peripsocidae), *Trichopsocus dalii* (McLachlan, 1867) (Trichopsocidae), *Hemineura dispar* Tetens, 1891 (Elipsocidae), and *Amphigerontia contaminata* (Stephens, 1836) (Psocidae) $2n = 16 + XX/X0$. In *Elipsocus moebiusi* Tetens, 1891 (Elipsocidae) $2n = 12 + XX/X0$. *Neopsocopsis hitricornis* (Reuter, 1893) (Psocidae) has $2n = 14 + XX/X0$, and *Kolbia quisquiliarum* Bertkau, 1883 (Amphipsocidae) has $2n = 14 + neo-XY/XX$. In addition, three seminal follicles per testis have been established in *V. oyamai*, *H. dispar*, *A. contaminata*, and *N. hitricornis* and one follicle in *P. golubae* and *T. dalii*. All the data available on psocopteran karyotypes are tabulated and shortly reviewed.

Key words: Psocoptera, karyotype, chromosome number, chromosomal mechanism of sex determination.

INTRODUCTION

Psocoptera are a hemimetabolous insect order, belonging with the orders Phthiraptera, Thysanoptera, Heteroptera, and Homoptera to the Cohort Paraneoptera. Within Psocoptera three suborders, Trogiomorpha, Troctomorpha, and Psocomorpha, have been accepted (Lienhard, 1998; Lienhard, Smithers, 2002).

Chromosome systems of Psocoptera are still not adequately explored, although some papers concerning psocopteran karyotypes have been published recently (Nokkala, Golub, 2002, 2006; Golub, 2004). Like the other Paraneoptera, the species of Psocoptera have holocentric chromosomes. So far, chromosome numbers have been established for 82 species from 48 genera and 21 families of Psocoptera.

The majority of species (72) belong to the most advanced suborder Psocomorpha.

The present study reports data on the karyotypes of 8 species from 8 genera and 6 families of Psocomorpha. The data on *Neopsocopsis* Badonnel, 1936, *Hemineura* Tetens, 1891 and *Kolbia* Bertkau, 1882 are the first ones for these genera. For 6 species data on numbers of seminal follicles are also given.

MATERIAL AND METHODS

The material studied is listed in Table 1.

For karyological studies, the specimens were fixed in a mixture of 96% ethanol and glacial acetic acid (3:1). Testes were dissected out of the abdomens and squashed on slides in a drop of 45% acetic acid. The prepara-



tions were made permanent by a dry ice technique (Conger, Fairchild, 1953). After cover slips were removed, slides were dehydrated in fresh 3:1, air-dried and stained by Feulgen-Giemsa procedure (Grozeva, Nokkala, 1996). Slides were treated in 1N HCl at room temperature for 20 min, hydrolysed in 1N HCl at 60° C for 7 min, stained with Schiff's reagent for 30 min, rinsed in distilled water and then, rinsed in Sorensen's phosphate buffer, pH 6.8. Finally, slides were stained with 5% Giemsa solution for 30 min. After staining, slides were rinsed briefly with distilled water, air dried, and mounted in Entellan.

RESULTS

Family Caeciliusidae

Valenzuela oyamai (Enderlein, 1906): $2n = 16 + XX/X0$.

Each testis contains three seminal follicles arranged in consecutive order on seminal duct. In MI, 8 autosomal bivalents and the X chromosome have been revealed (Fig. 1). The bivalents gradually decrease in size; the X chromosome is the smallest element of set. In the majority of cells, the X chromosome is situated at the periphery of the metaphase plate. The formula of the male diploid karyotype has

Table 1. Material used for chromosomal analysis.

Species	Locality, year of collection, number of specimens studied, feeding plants
<i>Valenzuela oyamai</i> (Enderlein, 1906) (Caeciliusidae)	Russia, Irkutsk Prov., Bolshie Koty, 2007, 12♂, undet. herbs
<i>Kolbia quisquiliarum</i> Bertkau, 1883 (Amphipsocidae)	Russia. Voronezh Prov., Hopersky State Reserve, 2005, 2♂, <i>Calamagrostis epigeios</i>
<i>Peripsocus golubae</i> Lienhard, 2006 (Peripsocidae)	Russia, Krasnodar Terr., 12 km N Adler, 2004, 2♂, <i>Buxus</i> sp.
<i>Trichopsocus dalii</i> (McLachlan, 1867) (Trichopsocidae)	Russia, Krasnodar Terr., 12 km N Adler, 2004, 5♂, undet. herbs
<i>Elipsocus moebiusi</i> Tetens, 1891 (Elipsocidae)	Finland, Kustavi, 2003. 4♂, deciduous trees Finland, Katanpää, 2003. 2♂, 3♀, deciduous trees Finland, Ruissalo, 2003, 3♂, 1♀, deciduous trees Russia. Voronezh Prov., Hopersky State Reserve, 2005, 1♂, 1♀, <i>Quercus</i> sp.
<i>Hemineura dispar</i> Tetens, 1891 (Elipsocidae)	Finland, vicinity of Turku, 2003, 11♂, deciduous trees
<i>Amphigerontia contaminata</i> (Stephens, 1836) (Psocidae)	Finland, vicinity of Turku, 1999, 4♂, dead coniferous branches
<i>Neopsocopsis hitricornis</i> (Reuter, 1893) (Psocidae)	Russia, republic of Altai, 40 km SE Chamal, 2006, 6♂, undet. coniferous

been determined as $2n = 17 (16 + X0)$.

Family Amphipsocidae

Kolbia quisquiliarum Bertkau, 1883: $2n = 14 + \text{neo-XY/XX}$.

In MI, 8 bivalents have been revealed (Fig. 2). In the majority of cells, one of the bivalents is clearly heteromorphic and could be considered the sex chromosome bivalent (Fig. 3). Apparently, the X chromosome is fused with an autosome resulting in a neo-XY sex chromosome system. The formula of the male diploid karyotype has been determined as $2n = 16 (14 + \text{neo-XY})$.

Family Peripsocidae

Peripsocus golubae Lienhard, 2006: $2n = 16 + \text{XX/X0}$.

Each testis contains one large seminal follicle. In MI, 8 autosomal bivalents and the X chromosome have been revealed (Fig. 4). The bivalents gradually decrease in size; the X chromosome is the smallest element of the set. The formula of the male diploid karyotype has been determined as $2n = 17 (16 + X0)$.

Family Trichopsocidae

Trichopsocus dalii (McLachlan, 1867): $2n = 16 + \text{XX/X0}$.

Each testis contains one large seminal follicle. In MI, 8 autosomal bivalents and the X chromosome have been revealed (Fig. 5). The bivalents gradually decrease in size; X chromosome is the smallest element of the set. In the majority of cells, the X chromosome is situated at the periphery of the metaphase plate. In MII homologues segregate regularly and chromosomal plates with 8 and 9 univalent chromosomes respectively, have been observed (Fig. 6). The formula of the male diploid karyotype has been determined as $2n = 17 (16 + X0)$.

Family Elipsocidae

Elipsocus moebiusi Tetens, 1891: $2n = 12 + \text{XX/X0}$.

In MI, 6 autosomal bivalents and the X chromosome have been revealed (Fig. 7). One of the bivalents is nearly twice as large as any other. The X chromosome is close in size to smallest half-bivalents. In the majority of cells, the X chromosome is situated at the periphery of the metaphase plate. The formula of the male diploid karyotype has been determined as $2n = 13 (12 + X0)$. A female mitotic metaphase (Fig. 8) displays 12 chromosomes with one large chromosomal pair. Sex chromosomes are not distinguished.

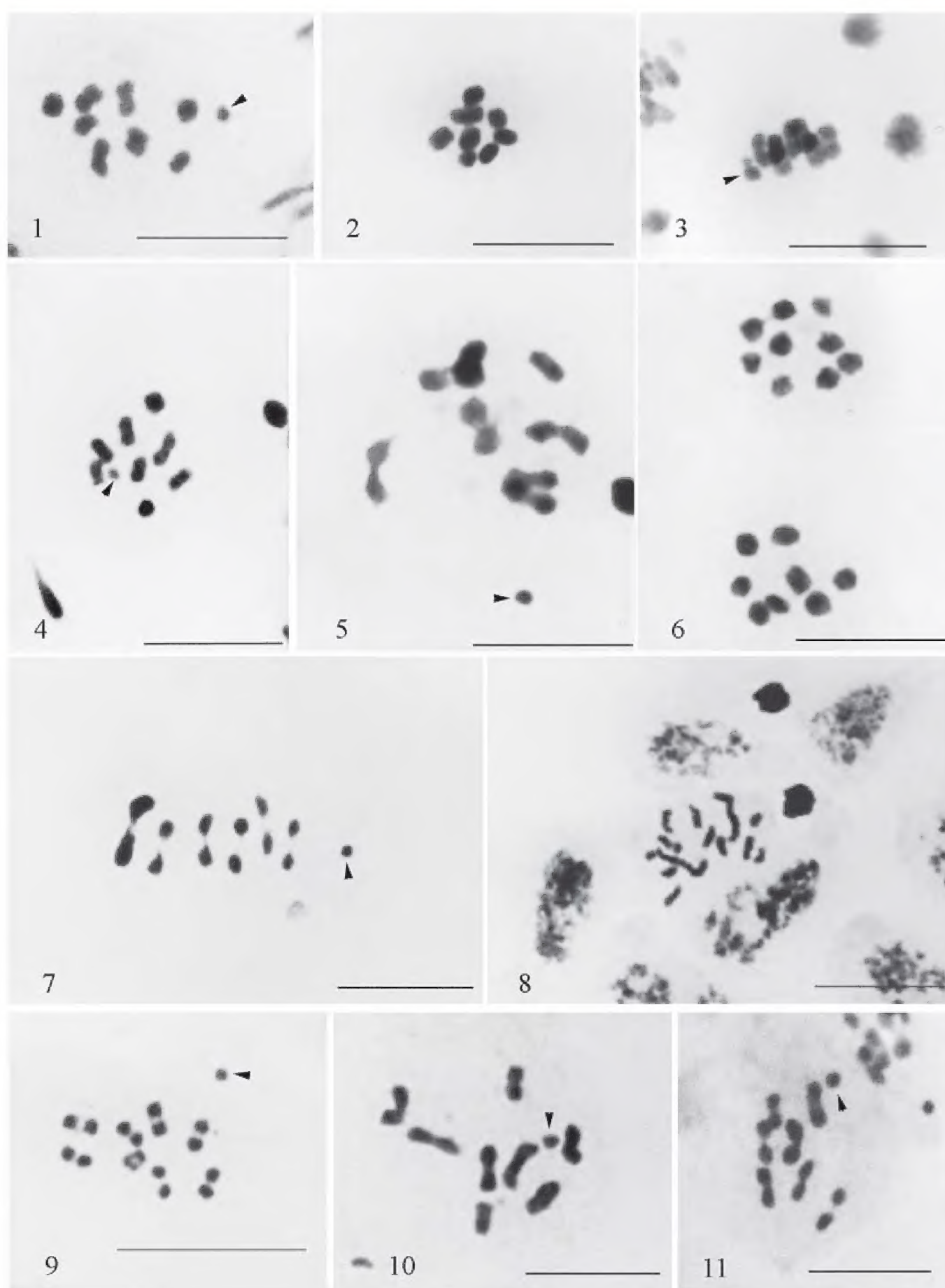
Hemineura dispar Tetens, 1891: $2n = 16 + \text{XX/X0}$.

Each testis contains three seminal follicles arranged in consecutive order on seminal duct. In MI, 8 autosomal bivalents and the X chromosome have been revealed (Fig. 9). The bivalents gradually decrease in size; the X chromosome is close in size to the middle-sized half-bivalents. In the majority of cells, the X chromosome is situated at the periphery of the metaphase plate. The formula of the male diploid karyotype has been determined as $2n = 17 (16 + X0)$.

Family Psocidae

Amphigerontia contaminata (Stephens, 1836): $2n = 16 + \text{XX/X0}$.

Each testis contains three seminal follicles which are terminally brought together on seminal duct. In MI, 8 autosomal bivalents and the X chromosome have been revealed (Fig. 10). The bivalents gradually decrease in size; the X chromosome is close in size to the middle-sized half-bivalents. The formula of the male diploid karyotype has been determined as $2n = 17 (16 + X0)$.



Figs 1-11. Chromosome complements of Psocomorpha. **1** - *Valenzuela oyamai*. Male meiotic metaphase I showing 8 autosomal bivalents and univalent X chromosome. **2-3** - *Kolbia quisquiliarum*. Male meiotic metaphase I showing 8 bivalents. One of the bivalents is clearly heteromorphic (better represented in Fig. 3). **4** - *Peripsocus golubae*. Male meiotic metaphase I showing 8 autosomal bivalents and univalent X chromosome. **5-6** - *Trichopsocus dalii*; **5** - Male meiotic metaphase I showing 8 autosomal bivalents and univalent X chromosome; **6** - Male meiotic metaphases II showing 8 (autosomes only) and 9 (autosomes + X chromosome) elements. **7-8** - *Elipsocus moebiusi*; **7** - Male meiotic metaphase I showing 6 autosomal bivalents and univalent X chromosome; **8** - Female mitotic metaphase showing 12 chromosomes. **9** - *Hemineura dispar*. Male meiotic metaphase I showing 8 autosomal bivalents and univalent X chromosome. **10** - *Amphigerontia contaminate*. Male meiotic metaphase I showing 8 autosomal bivalents and univalent X chromosome. **11** - *Neopsocopsis hitricornis*. Male meiotic metaphase I showing 7 autosomal bivalents and univalent X chromosome. Sex chromosomes are indicated by arrowheads. Bar = 10 μ m.

Neopsocopsis hitricornis (Reuter, 1893): $2n = 14 + XX/X0$.

Each testis contains three seminal follicles which are terminally brought together on seminal duct. In MI, 7 autosomal bivalents and the X chromosome have been revealed (Fig. 11). One of the bivalents is noticeably larger than others. The X chromosome is close in size to the middle-sized half-bivalents. In the majority of cells, X chromosome is situated at the periphery of the metaphase plate. The formula of male diploid karyotype has been determined as $2n = 15 (14 + X0)$.

DISCUSSION

With our new results, the karyotypes of 90 psocopteran species from 51 genera and 21 families are presently known (Table 2). The five species studied in the present work, *Valenzuela oyamai* (Caeciliusidae), *Peripsocus golubae* (Peripsocidae), *Trichopsocus dalii* (Trichopsocidae), *Hemineura dispar* (Elipsocidae), and *Amphigerontia contaminata* (Psocidae), share $2n = 16 + XX/X0$. The same chromosome complement is characteristic of 72 bisexual and diploid parthenogenetic species of Psocoptera. For triploid parthenogenetic species the chromosome number $3n = 27$ was reported (Nokkala, Golub, 2002, 2006), which number comprises 18 chromosomes of the diploid complement and one additional haploid chromosomal set. Thus, our new results confirm the high stability of chromosome numbers in Psocoptera (Wong, Thornton, 1966; Mesa et al., 1991; Golub, 1999).

Three species studied here show the deviating karyotypes. In *Elipsocus moebiusi* (Elipsocidae) $2n = 12 + XX/X0$. This chromosome number is the lowest one in Psocoptera, and previously was reported only for *Loensia variegata* Latreille, 1799 (Psocidae) (Golub, 2004). Two other studied species from the genus *Elipsocus* Hagen, 1866 are characterized

by $2n = 16 + XX/X0$ (Table 2).

Neopsocopsis hitricornis (Psocidae) was shown to have $2n = 14 + XX/X0$. These are the first karyological data on the genus as a whole. In the family Psocidae 26 species have been karyologically studied so far, among them three species also display $2n = 14 + XX/X0$ (Table 2).

Kolbia quisquiliarum (Amphipsocidae) has $2n = 14 + neo-XY/XX$, and these are the first karyological data on the genus as a whole. Previously, the neo-XY-mechanism of sex determination has been found in *Amphipsocus japonicus* Enderlein, 1906 (Amphipsocidae) (Golub, Nokkala, 2001). Although this derivative sex-determining mechanism has never been reported for any other families, karyological data are still inadequate to consider this mechanism as characteristic of the family Amphipsocidae.

The karyotype with $2n = 16 + XX/X0$ is prevalent and considered ancestral for Psocoptera, including the advanced suborder Psocomorpha (Wong, Thornton, 1966; Golub, 1999). On the basis of all karyological data available, it may be suggested that in Psocomorpha chromosome numbers tend to decrease (Table 2). Thus, the diploid chromosome number decreases from $2n = 17$ (in males of 22 species) to $2n = 15$ (in 3 species) and $2n = 13$ (one species) in the family Psocidae, as well as from $2n = 17$ (in 5 species) to $2n = 13$, (one species) in the family Elipsocidae. Both studied species of the family Amphipsocidae have $2n = 16$ and neo-XY/XX mechanism of sex determination. Only in the family Stenopsocidae the chromosome number increases from $2n = 17$ (in 3 species) to $2n = 23$ (in 2 species). Data on karyotypes in other families are restricted to 1-4 species all of which have the modal karyotype $2n = 17 + X0$. In contrast, chromosome numbers in the primitive suborder Trogiomorpha seem to show a tendency to increase. Only

Table 2. Chromosome numbers in Psocoptera. * parthenogenetic species.

Taxon	2n	References
TROGIOMORPHA		
Trogiidae		
<i>Lepinotus inquilinus</i> Heyden, 1850	16+XX/X0	Wong, Thornton, 1966
<i>L. reticulatus</i> Enderlein, 1905 *	18	Jostes, 1975
<i>Trogium pulsatorium</i> (Linnaeus, 1758)	20+XX/X0	Meinander et al., 1974
Psoquillidae		
<i>Psoquilla marginepunctata</i> Hagen, 1865	18+XX/X0	Wong, Thornton, 1966
Psyllipsocidae		
<i>Psocatropos</i> sp.	28+XX/X0	Wong, Thornton, 1966
<i>Dorypteryx domestica</i> (Smithers, 1958)	28+XX/X0	Golub, Kučerová, 2008
TROCTOMORPHA		
Amphientomidae		
<i>Seopsocus acuminatus</i> Roesler, 1940	16+XX/X0	Mesa et al., 1991
<i>Seopsis</i> sp.	14+XX/X0	Wong, Thornton, 1966
Liposcelidae		
<i>Liposcelis divergens</i> Badonnel, 1943 *	16+XX	Goss, 1954
<i>L. bostrychophilus</i> Badonnel, 1931 *	14+XX	Jostes, 1975
PSOCOMORPHA		
Epipsocidae		
<i>Epipsocus lucifugus</i> (Rambur, 1842)	16+XX/X0	Golub, 1999
Caeciliusidae		
<i>Caecilius fuscopterus</i> (Latreille, 1799)	16+XX/X0	Golub et al., 1996
<i>Caecilius</i> sp.1	16+XX/X0	Zefa et al., 1996
<i>Caecilius</i> sp.2	16+XX/X0	Wong, Thornton, 1966
<i>Asiocaecilius singaporensis</i> (Enderlien, 1903)	16+XX/X0	Wong, Thornton, 1966
<i>Dypsocus</i> sp.	16+XX/X0	Wong, Thornton, 1966
<i>Valenzuela oyamai</i> (Enderlein, 1906)	16+XX/X0	present study
<i>V. burmeisteri</i> (Brauer, 1876)	16+XX/X0	Meinander et al., 1974; Golub, 1999
<i>V. gynapterus</i> (Tetens, 1891)	16+XX/X0	Golub, 1998
<i>V. labinae</i> Lienhard, 2006 *	24+XXX	Nokkala, Golub, 2006
<i>V. flavidus</i> (Stephens, 1836) *	16+XX; 24+XXX	Meinander et al., 1974; Nokkala, Golub, 2002
<i>V. piceus</i> (Kolbe, 1882)	16+XX/X0	Golub, 1999
<i>Enderleinella obsoleta</i> (Stephens, 1836)	16+XX/X0	Meinander et al., 1974; Golub, 1999
Stenopsocidae		
<i>Graphopsocus cruciatus</i> (Linnaeus, 1768)	16+XX/X0	Golub et al., 1996
<i>Stenopsocus immaculatus</i> (Stephens, 1836)	16+XX/X0	Golub et al., 1996
<i>S. aphidiformis</i> Enderlein, 1906	22+XX/X0	Golub, 2004
<i>S. lachlani</i> Kolbe, 1880	22+XX/X0	Meinander et al., 1974; Golub, 1999
Amphipsocidae		
<i>Amphipsocus japonicus</i> Enderlein, 1906	14+XX/Neo-XY	Golub, Nokkala, 2001
<i>Kolbia quisquiliarum</i> Bertkau, 1882	14+XX/Neo-XY	present study

Table 2 (continuation).

Lachesillidae		
<i>Lachesilla pedicularia</i> (Linnaeus, 1758)	16+XX/X0	Golub, 2004
<i>L. quercus</i> (Kolbe, 1880)	16+XX/X0	Golub et al., 1996
<i>L. tanaidana</i> Roesler, 1953	16+XX/X0	Golub, 2004
Ectopsocidae		
<i>Ectopsocus briggzi</i> McLachlan, 1899	16+XX/X0	Golub, 2004
<i>E. maindroni</i> Badonnel, 1935	16+XX/X0	Wong, Thornton, 1966
<i>E. meridionalis</i> Ribaga, 1904 *	24+XXX	Nokkala, Golub, 2006
<i>Ectopsocopsis cryptomeriae</i> Enderlein, 1907	16+XX/X0	Wong, Thornton, 1966
Peripsocidae		
<i>Diplopsocus fasciatus</i> (Thornton, 1959)	16+XX/X0	Wong, Thornton, 1966
<i>Peripsocus golubae</i> Lienhard, 2006	16+XX/X0	present study
<i>P. quercicola</i> Enderlein, 1906	16+XX/X0	Wong, Thornton, 1966
<i>P. alboguttatus</i> (Dalman, 1823)	16+XX/X0	Golub, 1998
<i>P. parvulus</i> Kolbe, 1880	16+XX/X0	Golub, 1999
<i>P. phaeopterus</i> (Stephens, 1836)	16+XX/X0	Golub, 1998
<i>P. subfasciatus</i> (Rambur, 1842) *	24+XXX	Nokkala, Golub, 2002
<i>Peripsocus</i> sp.	16+XX/X0	Wong, Thornton, 1966
Pseudocaecilliidae		
<i>Pseudocaecilius hirsutus</i> (Thornton, 1961)	16+XX/X0	Wong, Thornton, 1966
<i>Pseudocaecilius maculosus</i> Enderlein, 1907	16+XX/X0	Golub, Nokkala, 2001
Trichopsocidae		
<i>Trichopsocus dalii</i> (McLachlan, 1867)	16+XX/X0	present study
<i>T. brincki</i> Badonnel, 1963	16+XX/X0	Golub, Nunes, 2007
<i>T. clarus</i> (Banks, 1908)	16+XX/X0	Golub, Nunes, 2007
Archipsocidae		
<i>Archipsocus</i> sp.	16+XX/X0	Wong, Thornton, 1966
Ptiloneuridae		
<i>Triplocania caudata</i> New, 1980	16+XX/X0	Zefa et al., 1996
Elipsocidae		
<i>Elipsocus moebiusi</i> Tetens, 1891	12+XX/X0	present study
<i>E. abdominalis</i> Reuter, 1904	16+XX/X0	Meinander et al., 1974
<i>E. pumilis</i> (Stephens, 1861)	16+XX/X0	Golub, 2004
<i>E. westwoodi</i> McLachlan, 1867	16+XX/X0	Meinander, et al., 1974
<i>Hemineura dispar</i> Tetens, 1891	16+XX/X0	present study
<i>Reuterella helvimacula</i> (Enderlein, 1901)	16+XX/X0	Meinander et al., 1974
Philotarsidae		
<i>Philotarsus picicornis</i> (Fabricius, 1793)	16+XX/X0	Golub, 1999; Nokkala, Golub, 2002
<i>Aaroniella badonneli</i> (Danks, 1950) *	16+XX	Nokkala, Golub, 2006
<i>Haplophallus orientalis</i> Thornton, 1959	16+XX/X0	Wong, Thornton, 1966
Mesopsocidae		
<i>Mesopsocus honkongensis</i> Thornton, 1959	16+XX/X0	Wong, Thornton, 1966
<i>M. unipunctatus</i> (Muller, 1764)	16+XX/X0	Meinander et al., 1974; Golub, 1999
<i>M. laticeps</i> (Kolbe, 1880)	16+XX/X0	Golub, 1999
Hemipsocidae		
<i>Hemipsocus</i> sp.	16+XX/X0	Wong, Thornton, 1966

Table 2 (conclusion).

Psocidae		
<i>Atlantopsocus adustus</i> (Hagen, 1865)	16+XX/X0	Golub, Nunes, 2007
<i>Amphigerontia contaminata</i> (Stephens, 1836)	16+XX/X0	present study
<i>A. bifasciata</i> (Latreille, 1799)	16+XX/X0	Golub, 2004
<i>A. jezoensis</i> Okamoto, 1907	14+XX/X0	Golub, 2004
<i>Blaste conspurcata</i> (Rambur, 1842)	16+XX/X0	Golub et al., 1996
<i>Brachinodiscus</i> cf. <i>lepidus</i> (Banks, 1920)	16+XX/X0	Zefa et al., 1996
<i>Cerastipsocus venosus</i> (Burmeister, 1839)	16+XX/X0	Boring, 1913
<i>C. fuscipennis</i> (Burmeister, 1839)	16+XX/X0	Mesa et al., 1991
<i>Hyalopsocus contrarius</i> Reuter, 1893	16+XX/X0	Golub et al., 1996
<i>Loensia moesta</i> (Hagen, 1861)	16+XX/X0	Golub et al., 1996
<i>L. variegata</i> (Latreille, 1799)	12+XX/X0	Golub, 2004
<i>L. picicornis</i> (Stephens, 1836)	16+XX/X0	Meinander et al., 1974
<i>Neopsocopsis hitricornis</i> (Reuter, 1893)	14+XX/X0	present study
<i>Psococerastis gibbosa</i> (Sulzer, 1766)	16+XX/X0	Golub et al., 1996
<i>P. sinensis</i> Thornton, 1960	16+XX/X0	Wong, Thornton, 1966
<i>Metylophorus nebulosus</i> (Stephens, 1836)	14+XX/X0	Meinander et al., 1974; Golub, 1999
<i>Psocus leidy</i> Aaron, 1886	16+XX/X0	Golub et al., 1996
<i>Sigmatoneura kolbei</i> Endrelein, 1906	16+XX/X0	Golub, 2004
<i>Ptycta incurvata</i> Thornton, 1960	16+XX/X0	Wong, Thornton, 1966
<i>Psococerastis interrupta</i> New, 1972	16+XX/X0	Zefa et al., 1996
<i>P. nr reticulata</i> New, 1972	16+XX/X0	Zefa et al., 1996
<i>Trichadenotecnum majus</i> (Kolbe, 1880) *	16+XX	Nokkala, Golub, 2002
<i>T. medium</i> Thornton, 1961	16+XX/X0	Wong, Thornton, 1966
<i>T. sexpunctatum</i> (Linnaeus, 1758)	16+XX/X0	Golub, 2004
<i>T. sinuatum</i> New, 1972	16+XX/X0	Zefa et al., 1996
<i>Atrichadenotecnum nudum</i> (Thornton, 1961)	16+XX/X0	Wong, Thornton, 1966

two species of the suborder display $2n = 17$ in males, whereas all other studied species have the higher chromosome numbers: $2n = 19, 21$ and 29 in males. Karyological data on Troctomorpha are presently extremely scanty. In four so far studied species of the suborder $2n = 14 + XX/X0$ and $2n = 16 + XX/X0$ have been found (Table 2).

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REFERENCES

- Boring A.M. 1913.** The odd chromosome in *Cerastipsocus venosus* // *Biol. Bull.* 24: 125-132.
- Conger A.D., Fairchild L.M. 1953.** A quick-freeze method for making smear slides permanent // *Stain Tech.* 28: 289-293.
- Golub N.V. 1998.** Karyotypes and testes structure in Psocomorpha (Psocoptera), (pp. 90-91) // Medvedev G.S., Krivokhatskij V.A. (Eds.) *The problems of entomology in Russia. Proc. XI Symp. Russ. Entomol. Soc., St. Petersburg, September, 23-26, 1997. 1.* St. Petersburg. 243 p.

- Golub N.V. 1999.** Review of karyological data on psocids (Psocoptera) and description of karyotypes of 13 species // *Entomol. Obozr.* 78(2): 376-390. (In Russian, with English translation in *Entomol. Review.* 79: 412-424).
- Golub N.V. 2004.** The variability of chromosome numbers in Psocomorpha (Insecta: Psocoptera) // *Caryologia.* 57: 67-71.
- Golub N.V., Grozeva S.M., Kuznetsova V.G. 1996.** Karyotypes of Psocoptera: a review and new data, (pp. 20-22) // Gokhman V.E., Kuznetsova V.G. (Eds.). *Karyosystematics of the invertebrate animals.* 3. Moscow. 88 p.
- Golub N.V., Nokkala S. 2001.** The karyotypes of two bark-lice species (Psocoptera, Psocomorpha, Amphipsocidae): the first description of neo-XY sex chromosome system in Psocoptera // *Folia Biol.* (Krakow). 49: 153-156.
- Golub N.V., Nunes E. 2007.** Karyotypes of three Psocoptera (Insecta) species from Madeira Island, Portugal // *Comp. Cytogenet.* 1(2): 155-158.
- Golub N.V., Kučerová Z. 2008.** Karyotype and reproductive organs of male *Dorypteryx domestica* (Smithers, 1958) (Psocoptera: Trogiomorpha: Psyllipsocidae) // *Folia Biol.* (Kraków). 56(1-2): 21-23.
- Goss R.J. 1954.** Ovarian development of oogenesis in the book louse, *Liposcelis divergens* Badonnel (Psocoptera, Liposcelidae) // *Ann. Entomol. Soc. America.* 47: 180-207.
- Grozeva S., Nokkala S. 1996.** Chromosomes and their meiotic behavior in two families of the primitive infraorder Dipsocoromorpha (Heteroptera) // *Hereditas.* 125: 31-36.
- Jostes R.F. 1975.** A method for determining the chromosome number of parthenogenetic psocids (Insecta, Psocoptera) // *Cytologia.* 40: 553-555.
- Lienhard C. 1998.** Psocoptères Euro-Méditerranéens. Fauna de France, 83. Paris. 517 p.
- Lienhard C., Smithers C.N. 2002.** Psocoptera (Insecta) World Catalogue and Bibliography. Geneva. 745 p.
- Meinander M., Halkka O., Söderlund V. 1974.** Chromosomal evolution in the Psocoptera // *Not. Entomol.* 54: 81-84.
- Mesa A., Fontanetti C.S., Zefa E. 1991.** First contribution to the cytogenetics of Brazilian Psocoptera // *Rev. Brasileira Genet.* 14: 913-919.
- Nokkala S., Golub N. 2002.** Cytogenetical study of three parthenogenetic psocid species (Psocoptera, Psocomorpha) // *Hereditas.* 137: 198-201.
- Nokkala, S., Golub, N.V. 2006.** Automictic and apomictic parthenogenesis in psocids (Insecta: Psocoptera) // *Folia Biol.* (Krakow). 54(1-2): 19-22.
- Wong S.K., Thornton I.W.B. 1966.** Chromosome numbers of some Psocid genera (Psocoptera) // *Nature.* 211: 214-215.
- Zefa E., Fontanetti C.S., Mesa A. 1996.** Cytogenetics of six Brazilian species of Psocoptera // *Brazilian J. Genet.* 19: 597-598.

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